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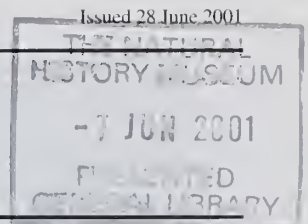
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Fossil pseudasturid birds (Aves, Pseudasturidae) from the London Clay

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SYNOPSIS. Fossil remains from the Lower Eocene (Ypresian) London Clay Formation of England are referred to the extinct higher-order group of birds, the Pseudasturidae Mayr. This material includes the specimen BMNH A 5193, referred by Harrison (1982) to the taxon '*Primobucco olsoni* Feduccia & Martin, previously the oldest published record of a piciform bird (barbets and relatives) known from the fossil record. The description of three-dimensionally preserved tarsometatarsi from the London Clay confirms the fully zygodactyl nature of the pseudasturid foot (fourth toe directed backwards).

INTRODUCTION

The extinct avian family Pseudasturidae was erected by Mayr (1998) for the reception of a number of small, zygodactyl, landbirds that are known from the Lower-Middle Eocene of Europe and North America. Mayr (1998) diagnosed this higher-taxon on the basis of a number of putatively derived (apomorphic) characters of the skull, vertebrae and limbs and included within the group two species from the Middle Eocene deposit of Grube Messel, Hessen, Germany (*Pseudastur macrocephalus* [Fig. 1] and an unnamed taxon), as well as the enigmatic taxon '*Primobucco olsoni* (Feduccia & Martin, 1976) known from the Eocene of North America, and from the London Clay (see Mayr, 1998).

In this paper, I present the descriptions of a number of fossil specimens from the London Clay Formation of England that are referable to the Pseudasturidae, as defined by Mayr (1998). Amongst this material is a proximal portion of tarsometatarsus (BMNH A 5193) that was classified by Harrison (1982) within the order Piciformes (barbets and relatives), previously the oldest published record for this group of modern birds. The three-dimensional preservation of the London Clay specimens serves to confirm the supposition of Mayr (1998) that the pseudasturid birds had a fully developed zygodactyl foot (fourth toe turned backwards to facilitate perching and climbing) with a prominent sehnenhalter or medial or plantar projection of the fourth trochlea (Steinbacher, 1935).

The fossil specimens discussed here are housed in the collections of The Natural History Museum, London, UK, (Palaeontology Department; BMNH A), the Forschungsinstitut Senckenberg, Frankfurt am Main, Germany (SMF), the Wyoming Dinosaur Center, Thermopolis, USA (collection POHL, examined in Frankfurt), and the Staatliches Museum für Naturkunde, Karlsruhe, Germany (SMNK). Recent osteological specimens examined during the course of this work are held in the ornithological collections of The Natural History Museum, Tring, Hertfordshire, UK (BMNH S). Anatomical nomenclature used follows Howard (1929) and Baumel & Witmer (1993).

SYSTEMATIC PALEONTOLOGY

Class AVES Linnaeus, 1758

Order INCERTAE SEDIS

Family PSEUDASTURIDAE Mayr, 1998

Genus and Species *INDET.*

Referred London Clay specimens

MATERIAL. BMNH A 6218 (Fig 2A), associated bones consisting of: a partially complete right scapula (lacking extreme lateral portion of extremitas caudalis); a partially complete right coracoid (lacking the processus procoracoideus, lateral extremity of processus acrocoracoideus and lateral portion of facies articularis sternalis); a proximal end of a left coracoid and portion of shaft; a proximal end of a right humerus and portion of shaft; a nearly complete left femur (lacking portions of condylus medialis, sulcus intercondylaris, condylus lateralis and crista trochanteris). BMNH A 6184 (Fig. 2F), a distal end of a left tarsometatarsus and portion of shaft.

GEOLOGICAL AGE AND LOCALITIES. BMNH A 6218 was collected from an unknown horizon within the London Clay Formation at Walton-on-the-Naze, Essex, England by Mr. W. George in 1977 (his original collectors number is unknown). BMNH A 6184 was collected from within division D–E of the London Clay Formation at Warden Point, Isle of Sheppey, Kent, England by Alleyn School (donated via Mr. Salmon) in 1983. The age of the Walton and Warden beds of the London Clay Formation (Bed A2; King, 1981) are approximately 54.4 Mya (after Harland *et al.*, 1990; Berggren *et al.*, 1995).

BMNH A 6218

SCAPULA (Fig. 2B). The blade of the scapula is broad and gently curved although the extremitas caudalis is lacking. The facies articularis humeralis is flat and ovate in form and is not excavated. The tuberculum coracoideum is small and obsolete, the acromion is rounded and blunt.

CORACOID (Fig. 2A). The processus acrocoracoideus is very abrupt and blunt with almost no point. The brachial tuberosity is very markedly folded over towards the processus procoracoideus; this tuberosity only extends laterally to level with the edge of the cotyla scapularis. The margin between the glenoid and scapular facets is raised and pronounced, the scapular facet is shallow but has a raised distal margin (much higher than the shaft). On both of the preserved coracoids, the extremity of the procoracoid process is broken but this does appear to have been flat laterally. There is a small foramen nervi supracoracoidei in the middle of the shaft distal to the sternal facet.

Overall, the coracoid shaft is straight, but there is a slight kink immediately distal to the foramen nervi supracoracoidei. The sternocoracoid impression is rectangular and shallowly excavated centrally; the distal borders of this impression are raised and the angulus



Fig. 1 *Pseudastur macrocephalus* holotype specimen (WDC-C-MG-94), covered with ammonium chloride to enhance contrast. Scale bar = 10mm. This figure reproduced from Mayr (1998) with permission, Forschungsinstitut Senckenberg.

medialis is pointed. The sternal facet is shallow, rectangular and located on the plane of the coracoid surface (not obliquely under the proximal end).

HUMERUS (Fig. 2D). In caudal view, the tuberculum dorsale (although broken distally) appears to point distally. The incisura capitis and tuberculum ventrale are obscured by sediment, although the latter appears to have been well developed. The fossa pneumotricipitalis is shallow, shelf-like and bordered laterally by a pronounced attachment for the musculus infraspinatus that is well developed and square-shaped. The lateral margin of the crista deltopectoralis is extremely curved (almost semi-circular) in outline, the crista bicipitalis meets the shaft at about 70 degrees; the crus dorsale fossae is obscured.

FEMUR (Fig. 2C). This is a very short and stocky element (relative to the preserved humeral length; see measurements). The fossa trochanteris is shallow and obsolete; the trochanter is not well developed and is rounded and blunt. The iliac facet is flat and in line with the head of the femur. The femoral head is turned distally and overhangs the shaft somewhat; the angle between the head and the shaft is about 90 degrees. The shaft is stocky and straight with little lateral curvature, there is no offset between the proximal and distal ends.

BMNH A 6184

TARSOMETATARSUS (Fig. 2F). A large foramen vasculare distale



Fig. 2 Pseudasturid specimens from the London Clay Formation. A–E, BMNH A 6218; A, portion of left coracoid; B, left scapula; C, left femur; D, portion of right humerus; E, right coracoid. F, BMNH A 6184, distal end of a left tarsometatarsus. G, BMNH A 6224, proximal right tarsometatarsus. All figures are $\times 2$.

is present that is ovate in outline. In plantar view, the surface of the tarsometatarsus is smoothly excavated distally. The trochlea metatarsi IV is broad anteriorly and bears a sehnenhalter (Steinbacher, 1935) that is not separated from the remainder of the trochlea by a groove (contrary to all known psittaciforms; Mayr & Daniels, 1998). On the lateral surface of the retroverted portion of trochlea metatarsi IV there is a marked and rounded prominence. The trochlea metatarsi III is broad and has a marked medial furrow that is bordered by two very prominent lateral ridges. This trochlea is separated from trochlea metatarsi II by a U-shaped depression. Trochlea metatarsi II is square in shape and very flat across the surface of the distal end (i.e. knuckle-view).

Measurements

BMNH A 6218: humerus, total preserved length – 15mm, width of caput humeri – 2mm (insicura capitis infilled with sediment); right coracoid, total length – 14mm; length acrocoracoid to procoracoid – 1.2mm; proximal portion left coracoid, total preserved length – 8mm; length acrocoracoid to procoracoid – 1.3mm; left femur, total length – 16mm; right scapula, total length – 15mm.

BMNH A 6184: tarsometatarsus, total preserved length – 5.2mm

Tentatively referred London Clay specimens

MATERIAL. BMNH A 6224 (Fig. 2G), a proximal end of a right tarsometatarsus and portion of shaft (lacking the crista intermediae hypotarsi). BMNH A 5193 (Fig. 3), a proximal end of a right tarsometatarsus (referred to '*Primobucco*' *olsoni* Feduccia & Martin [Aves, Piciformes] by Harrison, 1982). A complete description of this element was provided by Harrison (1982).

GEOLOGICAL AGE AND LOCALITIES. Both the specimens BMNH A 6224 and A 5193 were collected from divisions D–E of the London Clay Formation at Warden Point, Isle of Sheppey, Kent, England (A 6224 collected and presented by Mr. D. Ward in 1982; A 5193 collected and presented by Mr. S. Silverstein in 1980). The age of these beds of the London Clay Formation is approximately 54.4 Mya (after Harland *et al.*, 1990; Berggren *et al.*, 1995).

BMNH A 6224

TARSOMETATARSUS (Fig. 2G). The proximal tarsometatarsus of BMNH A 6224 has a smoothly flattened medial shaft and a flat hypotarsus; the rims of the medial and lateral cotyles (cotylae mediale and laterale) extend distally to about the same level, the area intercotylaris is not raised significantly above the surface of the cotyles. On the proximal surface, both the cotyles are rounded in outline and have raised lateral rims. There are two preserved cristae intermediae hypotarsi. Two oblong proximal foramina are seen on the surface of the shaft; the outer one is somewhat larger but they are both at the same level on the proximal shaft.

Measurements

BMNH A 6224: proximal right tarsometatarsus, total preserved length – 5.2mm, medio-lateral width of hypotarsus – 2.2mm.

BMNH A 5193: proximal right tarsometatarsus, total preserved length – 7.8mm, width of distal end – 2.1mm, width at tibialis articus scar – 1.3mm (Harrison, 1982).

COMPARISONS AND REMARKS

Although the tarsometatarsi are clearly visible in dorsal view on the Messel pseudasturid specimens, detailed comparisons of this element are only possible between BMNH A 6184 and the well preserved tarsometatarsi of *Pseudastur macrocephalus* (WDC-C-MG-94; Mayr, 1998: text-fig. 1). *P. macrocephalus* and BMNH A 6184 are an almost exact match in terms of size and shape; in both specimens, trochlea metatarsi III is very broad (compared to the trochlea for metatarsals II and IV) and is extended far distally (especially with respect to trochlea metatarsi IV, which is small and located proximally on the shaft). Again, in both specimens there is a prominent medial furrow on the distal trochlea metatarsi III and trochlea metatarsi IV is turned somewhat plantarly to form a small phlange. Based on the characters outlined by Mayr (1998), the specimen BMNH A 6184 can be referred with confidence to the Pseudasturidae, especially because of the presence of the two characters: large foramen vasculare distale and trochlea metatarsi IV bearing a sehnenhalter (characters 10 and 11 of Mayr, 1998).

However, although BMNH A 6184 and the tarsometatarsus of *Pseudastur macrocephalus* are very much alike (and are certainly from very similar birds), there are a number of subtle differences: in *P. macrocephalus* the distal margin of the shaft is raised (the shaft of BMNH A 6184 is somewhat flatter and wider distal to the foramen vasculare distale; the foramen vasculare distale is more elongate and

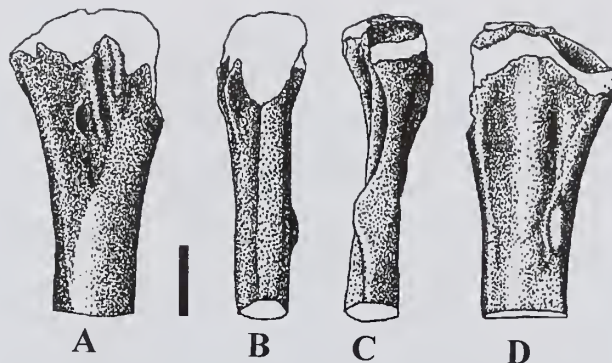


Fig. 3 Proximal end of right tarsometatarsus (BMNH A 5193) referred by Harrison (1982) to the Piciformes ('*Primobucco*' *olsoni* Feduccia & Martin; Primobucconidae). A, posterior; B, lateral; C, medial; D, anterior views. Unstippled areas are not preserved. Total length of specimen = 7.82 mm; scale bar = 2 mm. Redrawn after Harrison (1982).

teardrop shaped in *P. macrocephalus* (more circular in BMNH A 6184); and the trochlea metatarsi IV of BMNH A 6184 is wider and more robust. Lateral to the foramen vasculare distale (on the surface of the trochlea) there is a flat and shelf-like angled surface.

On the basis of the Messel material, Mayr (1998) was unable to conclusively demonstrate the fully or facultatively zygodactyl nature of members of the Pseudasturidae (cf. *Pseudastur macrocephalus*): 'whether *Pseudastur macrocephalus* was fully or facultatively zygodactyl is difficult to assess on the basis of the skeletons from Messel known so far'. This is because in all the known Messel specimens, the anterior portion of the trochlea metatarsi IV is obscured as a result of compaction during preservation (Mayr, 1998). On the basis of BMNH A 6184, an entirely uncrushed specimen, it is possible to confirm the observation of Mayr (1998) that members of this extinct clade had developed a fully zygodactyl foot morphology (Fig. 4).

BMNH A 6224 and A 5193 can be tentatively referred to the Pseudasturidae on the basis of comparisons with *Pseudastur macrocephalus* (WDC-C-MG-94). Both of the London Clay specimens are of a similar size and correspond with the proximal tarsometatarsi of WDC-C-MG-94 (although they are slightly larger; see measurements). As in WDC-C-MG-94, the foramina vascularia proximalia are at the same level on the shaft, the inner one being somewhat larger. The hypotarsal areas in the three specimens are identical (although only the crista medialis hypotarsi is seen clearly in WDC-C-MG-94); this protrudes over the fossa infracotylaris dorsalis and the impressio ligamentis collateralis is pronounced in all three specimens.

Harrison (1982) referred BMNH A 5193 (Fig. 3) to the taxon '*Primobucco*' *olsoni* (quotation marks added after Mayr, 1998) within the extinct family Primobucconidae erected by Feduccia & Martin (1976) within the order Piciformes. He noted that 'within that family, it [BMNH A 5193] appears to match in characters and size the corresponding bone of *Primobucco olsoni* Feduccia & Martin, as described and figured by them'. Harrison (1982) provided no further indication of what these characters might be. Referral of this specimen to within the order Piciformes cannot be confirmed with any degree of confidence: although monophyly of the order has been supported on the basis of a number of characters (i.e. zygodactyl foot, type IV flexor tendons, and m. flexor hallucis longus three-headed; Simpson & Cracraft, 1981; Swierczewski & Raikow, 1981; Raikow & Cracraft, 1983), none of these can be confirmed for